

THE USE OF ARM SUCKER NUMBER IN OCTOPODID SYSTEMATICS (CEPHALOPODA: OCTOPODA)

RONALD B. TOLL
DEPARTMENT OF BIOLOGY
THE UNIVERSITY OF THE SOUTH
SEWANEE, TENNESSEE 37375, U. S. A.

ABSTRACT

The average total number of suckers per arm for twelve species of octopodine cephalopods is presented in terms of the rate of sucker addition during growth. These data are shown to be useful for systematic analysis. The rate of sucker addition displays positive allometry relative to arm growth in early stages of development. Sucker addition slows to become negatively allometric in subadults and adults. New sucker morphogenesis ceases in the late stages of growth in some taxa resulting in an apparent species-specific sucker number. The hectocotylized arm displays a similar ontogenetic pattern of sucker addition.

Based on presumed reproductive isolation, general robustness, average arm sucker count (AASC), hectocotylized arm sucker count (HASC), and brooding mode, *Scaevurgus patagiatus* Berry, 1913 is removed from the synonymy of *S. unicolor* Orbnig, 1840 and is considered to be a separate species.

The total number of suckers on the arms of octopods is perhaps the second most salient meristic feature after the nominal character of the order (Octopoda = eight legs), which, being invariant among normal specimens, is of no systematic value among subordinal taxa. Counts of arm suckers occasionally were included as part of systematic descriptions and biological investigations of octopodid taxa, e.g. Féruissac and Orbnig (1834-48), Trochel (1857), Verrill (1882), Jatta (1896), Naef (1923), Winckworth (1928), Sasaki (1929), and Boletzky (1975), but most contemporary workers have ignored this character. Furthermore, I am unaware of any published account that compares octopodids, either inter- or intraspecifically, based on sucker counts or that employs these data in broader comparative studies at any taxonomic level. The limited use of either total number of arm suckers or the number of sucker rows in systematic treatments of octopod taxa is difficult to comprehend. The situation can at best be rationalized by appreciating the time required to count the suckers on each arm of the numerous specimens required to construct a significant data base. The total number of suckers per individual can range from several hundred to several thousand depending on species and maturity.

Most recently, Roper and Voss (1983), in their precedent setting guidelines for the description of cephalopod taxa, included arm sucker count (ASC) as a minimal requirement for the adequate taxonomic description of octopodids. However, not one of the three papers cited by these authors

as exemplary in octopod systematics include ASC data.

The arm sucker count of hatchling octopuses has been used as a specific-level systematic character (see Boletzky, 1977, 1984; Hochberg *et al.*, in press). The potential systematic value of arm sucker count in post-hatchling to adult octopodids remains inadequately investigated, an attribute shared by a large suite of other meristic and morphometric characters (e.g. gill lamellae number, penis morphology, alimentary tract anatomy, stellate ganglion morphology, etc.). The evaluation of ontogenetic rates of sucker morphogenesis also has been largely ignored, except for the most basic premises that larval octopods, whether benthic or planktonic, hatch with relatively few suckers compared to adults and that this sucker number increases with growth.

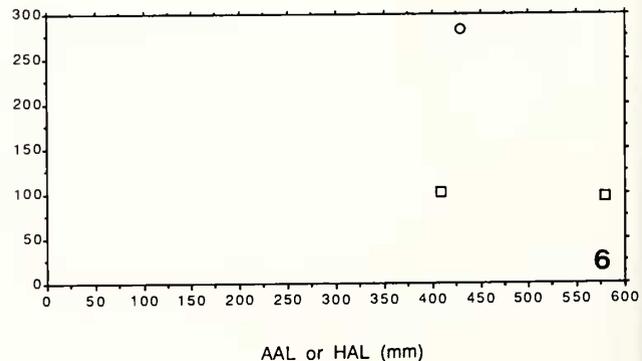
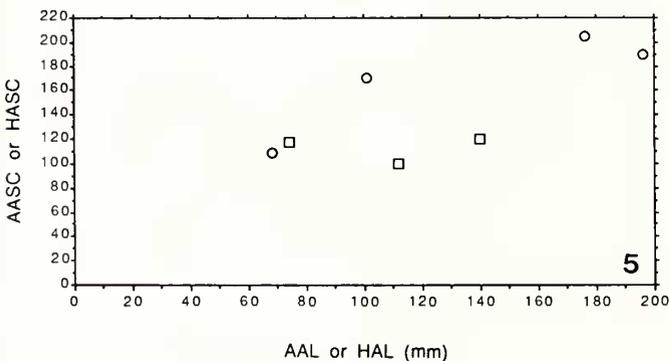
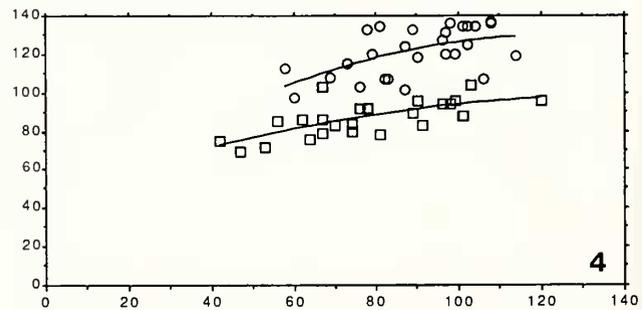
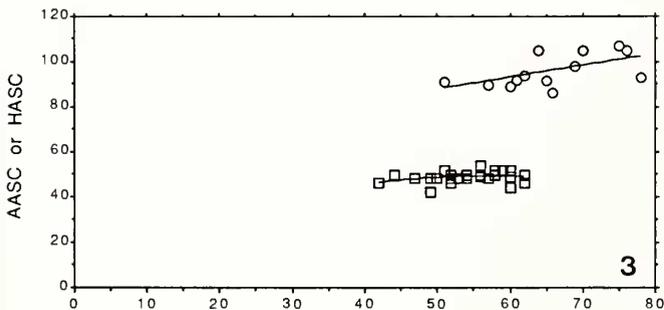
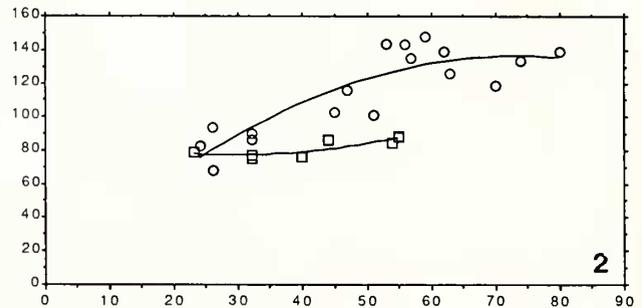
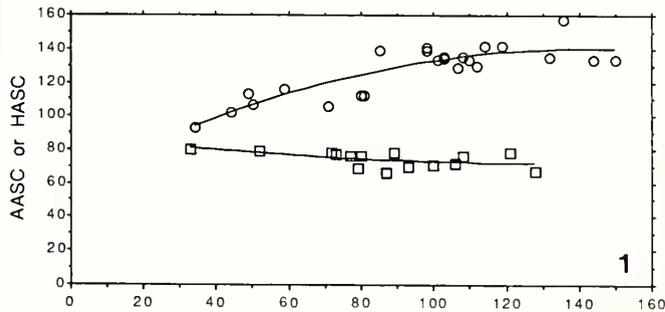
This paper presents a preliminary systematic survey of arm sucker counts in octopodine cephalopods. These results strongly suggest that average arm sucker counts can be valuable in systematic studies of the Octopodinae. The results also indicate that the rate of addition of new suckers shows a decidedly positive allometry with respect to arm growth in small animals. As a result, octopodids of relatively small body size precociously attain the majority of the adult complement of suckers. This phase is followed in late juveniles or early adults by negative allometry with a near to total cessation of addition of new suckers during the later stages of arm growth.

MATERIALS AND METHODS

The procedure used to count suckers was as follows. Suckers on each arm were counted starting at the mouth and moving to the tips. The relatively large suckers on the proximal two-thirds to three-quarters of the arm were counted using the unaided eye or an illuminated magnifier and passing a needle probe down the arm. Distally, where the suckers can be minute and densely packed, suckers were counted using a binocular microscope. A fine dissecting or insect pin was inserted into the arm as a marker during the transition between the two counting procedures. In all cases, sucker rudiments (anlagen), which appear as minute dome-like projections at the distal extremities of the arms, were counted as complete suckers. Suckers that were obviously missing, lost in combat with predators or prey or during capture, were counted as present. Only complete arms with the entire

distal tip intact were used to obtain sucker counts. Complete arms were considered 'available' and this term is used below. Arms regenerating from injury were excluded from consideration. To expedite counting, the number of sucker rows were counted and this value doubled to obtain the total sucker count for each individual arm. In cases of irregular sucker placement, a common artifact of preservation, this procedure could not be employed and it was necessary to count each sucker individually.

Arm lengths were measured using traditional methods with mechanical dividers and standard millimeter rules, following the guidelines re-established by Roper and Voss (1983). Average arm length (AAL) is the mean length of all available arms, with the exception of the hectocotylus. Average arm sucker count (AASC) is the mean of the number of suckers of all available arms with the exception of the hectocotylus. Both values are expressed to the nearest integer. Values



Figs. 1-6. Scattergrams of AASC vs. AAL and HASC vs. HAL for six species of Octopodinae [\circ = unmodified (nonhectocotylized) arms; \square = hectocotylized arm; each symbol represents a single animal]. **Fig. 1.** *Octopus burryi*. **Fig. 2.** *Octopus hummelincki*. **Fig. 3.** *Octopus selene*. **Fig. 4.** *Octopus digueti*. **Fig. 5.** *Octopus defilippi*. **Fig. 6.** *Octopus dofleini*.

reported here are from individual animals with at least two available arms. Hectocotylus arm length (HAL) and hectocotylized arm sucker count (HASC) were separately recorded. All specimens examined were preserved in alcohol and most, if not all, were previously fixed in formaldehyde. Shrinkage of the arms is assumed to have occurred as a result of this chemical treatment (see Andriuguetto and Haimovici, 1988). Scattergrams and statistical regression analyses were performed using a MacIntosh Plus[®] micro-computer with the statistical program Statworks 512+[®].

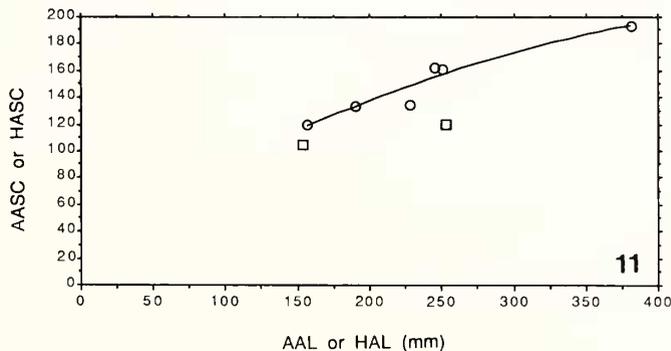
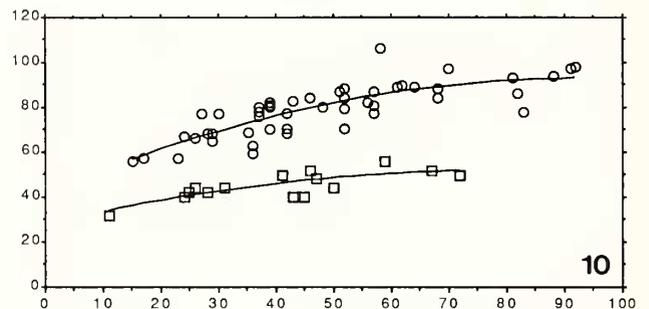
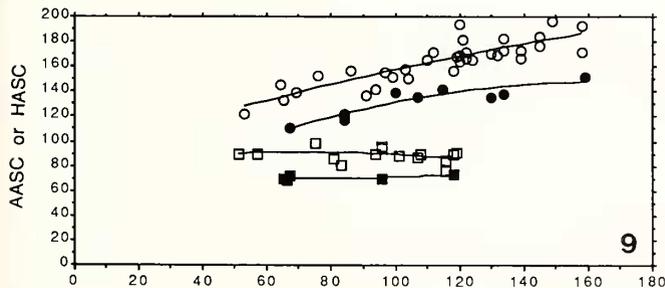
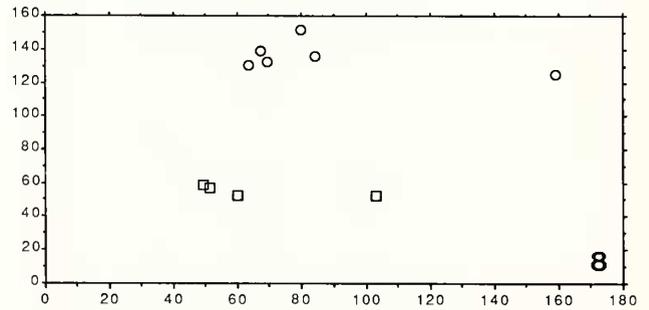
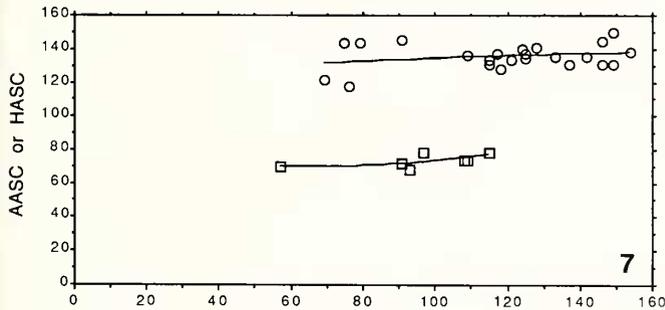
RESULTS AND DISCUSSION

AAL, AASC, HAL, and HASC data from twelve species of octopodines are plotted in figures 1-11: *Octopus burryi* Voss; *O. hummelincki* Adam (= *O. filusus* Howell); *O. selene* Voss; *O. digueti* Perrier and Rochebrune; *O. defilippi* Verany; *O. dofleini*

(Wülker); *Pteroctopus tetracirrhus* (delle Chiaje); *Robsonella fontanianus* (Orbigny); *Scaevargus unicolor* Orbigny; *S. patagiatus* Berry; *Hapalochlaena* cf. *maculosa* (Hoyle); *Cistopus indicus* (Orbigny). Second-order regression lines are included for all data sets where $n \geq 5$ (except *R. fontanianus*).

Preliminary regression analyses used each available arm on all animals as a separate datum, with the exception of the hectocotylus. The resultant scattergrams, combined with a basic understanding of octopod growth, showed that, for any one animal, arm sucker counts and arm lengths are autocorrelated, thereby jeopardizing the statistical validity of the regression. Individual averaging of the two data sets from each animal greatly reduced the size of the resulting data sets but served to enhance their robustness.

Larval and small juvenile specimens are absent from the present analyses, a reflection of the relative lack of representation of small individuals in museum collections and



Figs. 7-11. Scattergrams of AASC vs. AAL and HASC vs. HAL for six species of Octopodinae [○ = unmodified (nonhectocotylized) arms; □ = hectocotylized arm; each symbol represents a single animal]. **Fig. 7.** *Pteroctopus tetracirrhus*. **Fig. 8.** *Robsonella fontanianus*. **Fig. 9.** *Scaevargus unicolor* (darkened symbols), *Scaevargus patagiatus* (open symbols). **Fig. 10.** *Hapalochlaena* cf. *maculosa*. **Fig. 11.** *Cistopus indicus*.

the difficulty of identification of young octopodines. Therefore, the size ranges of some taxa included here are restricted to sub-adults and adults. Nonetheless, compared to the rate of arm growth (as a linear measurement), addition of arm suckers shows a distinct positive allometry during early growth stages. Small, presumably young, individuals have a disproportionately large percentage of their full adult complement of suckers. In *Octopus burryi* (Fig. 1), animals from 44-59 mm AAL had attained an average of 80.6% of the mean sucker count of animals from 98-119 mm AAL. Similar trends are seen in *O. hummelincki* (Fig. 2), *O. digueti* (Fig. 4), *O. defilippi* (Fig. 5), *Scaevargus patagiatus*, *S. unicolor* (Fig. 9), *Hapalochlaena cf. maculosa* (Fig. 10) and *Cistopus indicus* (Fig. 11). AASC in *Octopus selene* (Fig. 3), *Pteroctopus tetracirrus* (Fig. 7), and *Robsonella fontanianus* (Fig. 8) was statistically invariant over the size ranges reported here ($F = 2.29, 0.71, \text{ and } 1.81$, respectively; $p > .05$). Most of arm suckers in small individuals are rudimentary or minute and densely packed along the arm tip. Arm growth proceeds by elongation and expansion at the tips, while the anlagen located there enlarge and become more widely spaced. Data from larger specimens show a negative allometric relationship between sucker addition and arm growth. Indeed, in the final stages of arm growth, very few if any new sucker anlagen are added and the number of sucker rudiments and minute suckers is reduced as the suckers enlarge to reach their definitive sizes.

Average sucker number appears to reach a maximum value in each species in an apparent display of determinant growth. These maxima differ among the species examined; however, while they are presumed to be genetically determined, it seems unlikely that future study will elucidate non-overlapping species-specific values because of the large number of octopodine taxa. Average sucker number data can, however, assist in identification and taxonomic delineation of taxa from restricted geographical areas or that are otherwise morphologically similar (see below). Furthermore, the reduction of the number and density of rudimentary suckers along the distal tip of the arms could be valuable in recognizing environmentally induced precocious onset of sexual maturation in undersized individuals, a matter of considerable importance in studies of the structure of wild populations as well as artificially induced maturation of laboratory cultured animals. The change from positive to negative allometry could coincide with important ecological or developmental changes yet to be recognized.

It is well known that among octopodid taxa the characteristic length of the arms varies with respect to body size (mantle length). Data presented here suggest that AASC and HASC also vary with respect to arm length among different taxa, apparently a function of both sucker size and linear density (compare Figs. 5, 6, 8).

The hectocotylized arm of males presents a special case. Without exception HASC was lower than AASC for all individuals of all taxa examined. The rudimentary calamus and ligula form early in ontogenetic development from the distal tip of the arm which is partially devoid of sucker anlagen. By the onset of calamus and ligula morphogenesis, sucker morphogenesis has slowed considerably and soon ceases. There-

fore, the total sucker complement of the hectocotylized arm is less than, and is reached earlier in ontogeny than, any of the nonhectocotylized arms. Also, the most distal suckers are larger than those of the nonhectocotylized arms. HASC could, therefore, be a better taxonomic character despite its restriction to male individuals.

Each species appears to be characterized by a narrow range of values for HASC but, as with AASC, the large number of octopodid species probably precludes unique species-specific values. As with AASC, HASC also could be significant in restricted taxonomic applications (see below).

Reduction in length of the hectocotylized arm in comparison to the fellow arm of some taxa is well documented among the octopods. Also, the length of the modified portion of the arm varies among species, ranging from about 1 to 25% of the arm length. It is expected therefore, that the HASC varies among taxa independently of either general body size or lengths of the nonhectocotylized arms.

Analysis of AASC and HASC from a large collection of *Scaevargus* spp. ($n=44$) (Fig. 9) provided unexpected and taxonomically provocative results. The Atlantic Ocean (Florida, Caribbean, Mediterranean) and Pacific Ocean (Hawaii, Japan) populations show distinctly different and non-overlapping values of AASC for same-sized individuals and of HASC for all-sized individuals. *Scaevargus unicolor* was originally described by d'Orbigny (1840) from the Mediterranean Sea. Berry (1913) erected *Scaevargus patagiatus* from the Hawaiian Islands, supplementing his description the following year (Berry, 1914). Berry recognized the slightly larger size of the Hawaiian form and the zoogeographic (reproductive) separation of the two populations. He felt this was sufficient grounds to separate them at the species level. Robson (1929) synonymized *S. patagiatus* with *S. unicolor*, remarking that all differences between the two were insignificant except for the greater arm lengths in the Pacific form. Subsequently *S. unicolor* has been reported from the Indian Ocean (Robson, 1929) and the Western Atlantic Ocean (Voss, 1951). It has not been reported from the eastern Pacific Ocean. The genus is restricted to tropical and warm temperate waters.

The Atlantic and Pacific forms of *Scaevargus* are and probably have been reproductively isolated for an extended period of time, at least since the last closure of the Isthmus of Panama. The two populations differ substantially in maximum size, arm robustness, AASC, and HASC. Furthermore, the Pacific form is reported to brood its eggs by holding them within the web (W. Van Heukelem, pers. comm.; also see Boletzky, 1984), apparently an unusual behavior among octopodines (see Wells, 1978; Mangold, 1987). The more common practice of cementing the eggs to the substratum is displayed by the Atlantic form (Boletzky, 1984). I believe that the Pacific form merits the specific delineation recognized by Berry and correctly should be called *Scaevargus patagiatus* Berry, 1913.

The relative simplicity of counting arm suckers facilitates routine examination even by inexperienced workers. Replicate sucker counts performed by novice assistants in the present study were routinely close, typically with errors of 2% or less. The greatest source of potential error involves

the sucker rudiments on the arm tips. Some experience helps to standardize the counting procedure to include all true rudiments while excluding artifactual convolutions of the oral surface of the arm caused by fixation and/or preservation.

The use of total number of arm suckers rather than the number of sucker rows could be seen as arbitrary in view of the biserial sucker arrangement found in all octopodines. Indeed, in many cases sucker rows were counted and multiplied by two to obtain total sucker number. However, the uniformity of the biserial arrangement often is lost in portions of some arms in many individuals. Also, in larval specimens and in adults of some taxa, the first several adoral suckers are uniserial (Howell, 1868; Naef, 1923). Finally, the use of total counts will facilitate future comparisons with octopodids with uniserial sucker arrangements (e.g. Eledoninae), and does not suggest an unwarranted homology between a single row of suckers of the biserial octopodines and individual suckers of the eledonids and related groups.

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LITERATURE CITED

- Andrignetto, J. M. and M. Haimovici. 1988. Effects of fixation and preservation methods on the morphology of a loliginid squid (Cephalopoda: Myopsida). *American Malacological Bulletin* 6(2):213-217.
- Berry, S. S. 1913. Some new Hawaiian cephalopods. *Proceedings of the United States National Museum* 45:563-566.
- Berry, S. S. 1914. The Cephalopoda of the Hawaiian Islands. *Bulletin of the United States Bureau of Fisheries* 32:257-362.
- Boletzky, S. von. 1975. Le développement d'*Eledone moschata* (Mollusca, Cephalopoda) élevée au laboratoire. *Bulletin de la Société Zoologique de France* 100(3):361-367.
- Boletzky, S. von. 1977. Post-hatching behaviour and mode of life in cephalopods. *Symposia of the Zoological Society of London* No. 38:557-567.
- Boletzky, S. von. 1984. The embryonic development of the octopus *Scaevurgus uniccirrhus* (Mollusca, Cephalopoda). Additional data and discussion. *Vie et Milieu* 34(2/3):87-93.
- Férussac, M. and A. d'Orbigny. 1834-1848. *Histoire Naturelle Générale et Particulière des Céphalopodes Acétabulifères Vivant et Fossiles*. Paris. 366 pp.
- Hochberg, F. G., M. Nixon, R. Toll and R. Young. (In press). The Order Octopoda Leach, 1818. In: Larval and Juvenile Cephalopods. Proceedings of the First International Cephalopod Advisory Council Workshop, Banyuls, France, June, 1985.
- Howell, S. B. 1868. Descriptions of two new species of Cephalopods. *American Journal of Conchology* 3:239-241.
- Jatta, G. 1896. *Cephalopodi. Fauna und Flora des Gulfs von Neapel*. R. Friedländer and Sohn, Berlin. 268 pp.
- Mangold, K. 1987. Reproduction. In: *Cephalopod Life Cycles*, Vol. 11. *Comparative Reviews*. P. R. Boyle, ed. pp. 157-200, Academic Press, London.
- Naef, A. 1923. Die Cephalopoden. *Fauna et Flora des Golfes de Neapel* 35 (1), 863 pp.
- Orbigny, A. d'. 1840. In: Férussac, M. and A. d'Orbigny. *Histoire Naturelle Générale et Particulière des Céphalopodes Acétabulifères Vivant et Fossiles*. Paris. 366 pp.
- Robson, G. C. 1929. *A Monograph of the Recent Cephalopoda*, Part I, *Octopodinae*. British Museum, London. 236 pp.
- Roper, C. F. E. and G. L. Voss. 1983. Guidelines for taxonomic descriptions of cephalopod species. *Memoirs of the National Museum of Victoria* No. 44:49-63.
- Sasaki, M. 1929. Monograph of the dibranchiate cephalopods of the Japanese and adjacent waters. *Journal of the College of Agriculture, Hokkaido University* 20 (suppl. no.), 357 pp.
- Troschel, H. 1857. Bemerkungen über die Cephalopoden von Messina. *Archiv Naturgesch*, Berlin 23:41-76.
- Verrill, A. E. 1882. The Cephalopods of the Northeastern Coast of America. Report of the United States Fishery Commission for 1879:211-455.
- Voss, G. L. 1951. A first record of the cephalopod, *Scaevurgus uniccirrhus*, from the Western Atlantic. *Bulletin of Marine Science of the Gulf and Caribbean* 1 (1):64-71.
- Wells, M. J. 1978. *Octopus-Physiology and Behaviour of an Advanced Invertebrate*. Chapman and Hall, London. 417 pp.
- Winckworth, R. 1928. The hectocotylus of *Octopus octopodia* (L.) *Proceedings of the Malacological Society, London* 18:49-50.

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